Joel E. Cohen's Contributions to the Advancement of Science

Ernst Mayr, the eminent student of evolution, wrote in 1963: "The replacement of typological thinking by population thinking is perhaps the greatest conceptual revolution that has taken place in biology." Joel E. Cohen has invented important conceptual tools to sustain and extend that revolution. His path-breaking empirical studies using those tools increase the range of phenomena susceptible to scientific study. Here I summarize only the main points of his contributions in four areas: primate (human and non-human) social behavior, demography, community ecology, and the mathematical theory of non-negative matrices.

The idea that there might be similarities between the informal nonverbal behavior of humans and the unconstrained behavior of non-human primates has been commonplace. Cohen was the first to take the idea seriously enough to study quantitative data on casual social groups of several species of primates. He devised simple mathematical models that describe these data. Previous work on casual social groups in individual species had only considered the frequency distributions at equilibrium. These distributions are compatible with many different dynamic models. By recording the numbers of individuals in children's play groups every 30 seconds, Cohen was the first to observe the dynamics (trajectory in time) of systems of casual social groups, and the first to test in detail the dynamic assumptions of stochastic models for systems of social groups.

Cohen's models have predictive value. After he published his initial models, he went to Africa to observe baboons and test (successfully) the models further. His models also predict comparable observations of orang-utans and the distribution of the sizes of the 60 laboratories at Rockefeller University.

The potential applications of these models illustrate how basic research can be useful in unexpected ways. Cohen's models describe the distribution of occupancy of passenger vehicles in Los Angeles. Thus the models may be useful in trying to estimate how changes in car pooling habits might affect the volume of automobile traffic. Cohen's models also describe observations that were collected to study how viruses are transmitted among groups of monkeys. For epidemic theory, the models replace the assumption of homogeneous mixing of individuals by a more realistic description.

In demography, Cohen has proposed and studied in depth a new class of models for populations, such as human populations, in which individuals are categorized by age. Cohen's models are special cases of a model for products of random matrices. Cohen is the first to observe the relevance of this model to demography. He is also the first to give and apply an explicit procedure for calculating the long-run rate of growth of a product of random matrices and for finding the limiting distribution of age structure. These achievements are important mathematics. They also illuminate otherwise puzzling phenomena in the age structure and growth of populations with variable vital rates.

Cohen has proved a new class of ergodic theorems for populations in which birth and death rates contain some random variation over time. The classical ergodic theorems of demography are called "strong" and "weak." The strong ergodic theorem shows that the age structure of a population with birth and death rates that are constant over time converges to a fixed, so-called "stable" age structure. The weak ergodic theorem shows that if any two age-structured populations each have an identical sequence of (possibly changing) birth and death rates, the age structures of the two populations will become more and more alike; thus age structures forget their remote past. Cohen's ergodic theorems demonstrate the convergence in distribution of the age structure of a population whose birth and death rates are determined by a suitably ergodic Markov chain.

The potential practical significance of this work is that Cohen's models may provide improved means of preparing population projections for developed countries like the United States. Using his models, projections would take into account the apparently random fluctuations in past vital rates in order to attach well defined probabilities to estimates of the future.

In studying communities of species, ecologists have been publishing descriptions of food webs for nearly 80 years without much notion of whether there might be some invariant features in them. In another part of their minds, ecologists have also been thinking about niches, or how species make their livings, for nearly as long. In 1968, Cohen recognized a simple logical connection between the structural view of ecological communities given by food webs and the functional view given by the concept of niches. For ten years he collected and carefully analyzed food webs of natural communities. He found that real food webs are, under specified conditions, compatible with a structure of overlaps among niches that can be described in one dimension. This result provides the first empirical support for an assumption, widely made in ecological theory, that niche space can be studied as if it were one dimensional.

Each of these three examples brings new phenomena into the net of science with a quantitative crispness that is characteristic of Cohen's work. Now primate field workers pay attention to the details of the size distribution of the social groups they observe because Cohen's models give them a precise set of expectations. Now demographers are no longer bound to ignore the very real and important fluctuations in birth and death rates that stable population theory assumes away, because Cohen's demographic models show the important role that such fluctuations play. Now the food web as a whole is a worthwhile object of analysis, not merely of description. Cohen's findings of unexpected regularities strongly suggest that there may be more gold in those graphs.

Cohen reports a fourth area of his work, on novel properties of non-negative matrices, in mathematical terms. But the fine print of his papers shows that questions arising in the demography of age-structured populations led to his unexpected findings in a classical and well mined area of mathematics. Cohen showed that the spectral radius, or dominant eigenvalue, of a non-negative square matrix is a convex function of the main diagonal of the matrix. His first published proof used only results from the theory of determinants. Thus the result could have been proved 50 years ago if anybody had believed that such a surprisingly simple and beautiful fact were true. His second published proof uses a Feynman-Kac formula that arises in the theory of random evolutions, a product of the 1970's. Here he links a thoroughly modern branch of probability theory with a classical area of matrix algebra. Like the Perron-Frobenius theorem on non-negative matrices, Cohen's result is likely to be extensively generalized to positive operators and to be applied widely.

In this summary, I have not touched on Cohen's work on the epidemiology of malaria and schistosomiasis, his discovery of an extremely precise genetic control of cell number in the immune system of the fetal mouse, his demonstration--the first that is quantitatively defensible--of how the origins of replication in mammalian cell DNA are spatially organized. In these very diverse areas of research, Cohen's uniqueness and originality are that he thinks constantly and quantitatively in terms of populations as ensembles of interacting, biological units: what can populations reveal about the properties of individuals? what can individuals reveal about populations? what can be learned about and from omnipresent biological variability?